

ECOLOGY AND DISTRIBUTION OF THE INTRODUCED MOSS *CAMPYLOPUS INTROFLEXUS* (DICRANACEAE) IN WESTERN NORTH AMERICA

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ABSTRACT

Campylopus introflexus (Hedw.) Brid. is a moss native to the southern hemisphere and well documented as an invasive species throughout Europe. The species was first collected in North America in 1967 in Del Norte Co., California, and now occurs primarily in coastal areas from Santa Barbara Co. to southern British Columbia. Herbarium specimens were assembled and verified to document the distribution of the species in western North America. Collection dates of specimens indicate a rapid invasion along the coast north and south from the first record, with a slower establishment of inland populations. The species is most prevalent in coastal, foggy areas. Many of the populations are associated with anthropogenic environments, but several populations appear to be invading relatively undisturbed sites. These are mostly characterized by poor soils along the coast, with the largest populations associated with Bishop Pine forests and stabilized sand dunes. A brief summary of ecological literature documenting the European invasion of *C. introflexus* suggests that the species, especially in the presence of disturbance, has the potential to negatively impact native bryophyte, lichen, and vascular plant species.

Key Words: Bryophyte, British Columbia, California, introduced species, invasive species, Oregon, Washington.

The spread of invasive species is widely regarded as one of the primary threats to global biodiversity (Wilcove et al. 1998). While invasive vascular plants are the subject of active research, and millions of dollars in eradication efforts, the threats of more poorly known plants can go underappreciated because of a lack of basic documentation of their distribution and ecology.

Life history traits associated with invasive plant species are common among the bryophytes (hornworts, liverworts and mosses). Many bryophyte species are fast growing, excellent dispersers that rely heavily on asexual reproduction (During 1979). Despite this, very little information on bryophyte invasions exists in the literature (Söderström 1992). These gaps in knowledge include the basic parameters of invasions – for example, rates of spread and influence on native biota – that inform resource prioritization for the control of invasive vascular plant species.

One of the few cases of a bryophyte invasion that has been well studied is the European invasion of the southern hemisphere moss *Campylopus introflexus* (Hedw.) Brid. Introduced to Great Britain in 1941 (Richards 1963), it spread across the entire continent in less than fifty years, and is now widespread and locally common throughout Europe (Hassel and Söderström 2005; Klinck 2009). Over the last several decades, the species has been the source of ecological studies examining ecosystem impacts, habitat requirements and potential control methods throughout its European distribution as workers there move toward understanding the potential impacts of the species (reviewed by Klinck 2009).

The earliest collection of *C. introflexus* in North America was in northern California in 1967 (*D. Norris 8167* [CAS]). Since then it has spread north to Vancouver and south to the Channel Islands. The purpose of this study is to document the spread in western North America to date, to discuss the apparent ecological preferences of the species in western North America based on herbarium label data and field observations, and to briefly summarize the relevant European literature on the ecology and environmental impacts of the species.

MATERIALS AND METHODS

All collections of *Campylopus introflexus* from western North America at CAS, DUKE, UC, and UBC were examined, as well as collections from the personal herbaria of several bryologists. Field observations of California populations were made sporadically from 2007 to 2012. These included several populations in the Mendocino/Fort Bragg area, Mendocino Co. (near the putative introduction site), and populations at Salt Point State Park, Sonoma Co., the Monterey peninsula, Monterey Co., and Santa Cruz Island, Santa Barbara Co.

RESULTS AND DISCUSSION

Global Distribution and Ecology

Campylopus introflexus has a broad native distribution in the southern hemisphere between the latitudes of 22 and 66 (Gradstein and Sipman

1978). Common in Australia, New Zealand, South Africa, and southern South America, it is also present on many of the islands in the south Atlantic and Indian Oceans (Gradstein and Sipman 1978). The first verified record of the species from outside its native range is from Great Britain in 1941 (Richards 1963). From there it spread quickly across Europe and the current distribution spans from Iceland to Italy and from Estonia to Hungary (summarized by Klinck 2009). In Great Britain, where the spread was particularly well tracked, the species demonstrated the lag-period followed by rapid dispersal and colonization that is typical of invasive species (Hassel and Söderström 2005). From 1941 to about 1960, the geographic distribution remained very limited, but this was followed by exponential growth until saturation around 1980 (Hassel and Söderström 2005). It is unknown how the species was transported to Europe and whether there were single or multiple introductions. In some cases, molecular data can be useful in identifying the geographic origin of introduced bryophytes (Carter 2010), however molecular investigations in *Campylopus* using ITS and the chloroplast *atpB-rbcL* spacer have so far demonstrated insufficient variation to ascertain the origin of European and North American populations of *C. introflexus* (Stech and Dohrman 2004, Stech and Wagner 2005).

In Europe, where it is well studied, *C. introflexus* grows in a wide variety of habitats but only becomes dominant in sandy, acidic, soils (van der Meulen et al. 1987). In these environments, it can form extensive, dense turfs several centimeters thick. Some of the worst invasions in northern Europe are in stabilized dune communities where *C. introflexus* threatens fragile lichen dominated communities (Ketner-Oostra and Sykora 2008). In these systems, important factors for establishment, persistence and/or competitive advantage of *C. introflexus* include elevated soil C and N (Sparrus and Kooijman 2011), high soil organic matter (Hasse 2007; Daniels et al. 2008), and physical disturbance (Hasse 2007; Daniels et al. 2008). Under a high disturbance regime induced by ungulates, *C. introflexus* was documented overtaking a lichen dominated grassland and forming mono-dominant stands (Biermann and Daniels 1997), however a follow-up study ten years after removal of the ungulates demonstrated some recovery of the native lichen community (Daniels et al. 2008). *Campylopus introflexus* has also been shown to increase in frequency with an associated decrease in frequency of the moss *Polytrichum piliferum* (Hasse 2007), suggesting that it has the capacity to outcompete other moss species. Woody species can also be impacted by the presence of large turfs of *C. introflexus* through reduction of germination and establishment due to the inability of seedling roots to

penetrate through the tall turfs (Equihua and Usher 1993).

Distribution and Ecology in North America

In North America, *Campylopus introflexus* has been documented from California, Oregon, Washington, and southern British Columbia. Vouchers from the Aleutian Islands in Alaska and the Queen Charlotte Islands in British Columbia (*Schofield* 125265 [UBC, DUKE] and *Schofield* 33675 [DUKE], respectively) were misidentified specimens of other *Campylopus* species. The first specimen documenting *Campylopus introflexus* in western North America was collected by D. Norris in 1967 near Gasquet, Del Norte Co., California (Appendix 1). This collection precedes earlier reports citing 1971 as the first record (Frahm 1980; O'Brien 1999). At that time *Campylopus* in North America was poorly understood taxonomically, especially regarding separation of *C. introflexus* from *C. pilifer*, which is native to the southeastern U.S. and Mexico. After circumscriptions were clarified, it was realized that *C. introflexus* in western North America constitutes an introduced population (Gradstein and Sipman 1978; Frahm 1980, 2007).

The majority of known populations of *C. introflexus* in North America occur near the Pacific coastline within range of the marine influence (Fig. 1). For more than 20 years after the first voucher was collected, collections were mostly restricted to a narrow band of coastline within approximately 200 km north and south of the initial collection.

A noteworthy exception is the population from Lassen Volcanic National Park first documented by Showers in 1975 (Showers 1978, as *C. atrovirens* De Not.). That population has been the source of some confusion. The original collection, *Showers* 1909, is from Boiling Springs Lake, Plumas Co. not Lassen Co. as reported by Frahm (1980). Although Frahm (1980) cited the *Showers* 1909 specimen (currently housed at UC) as a voucher of *C. introflexus* in California, the specimen was annotated by him, dated November 1979, as *C. pilifer*. The specimen matches Frahm's (1980) morphological description of *C. introflexus* and the annotation on the specimen was apparently an error. O'Brien (1999) mentioned the discrepancy, but assumed that the literature report was erroneous (as opposed to the annotation). The population has recently been re-visited and a specimen collected (M. Hutten, personal communication). The population, which is clearly *C. introflexus* based on current interpretations of the morphological circumscriptions, is still established at Boiling Springs Lake and has expanded to the nearby Terminal Geyser (Appendix 1).

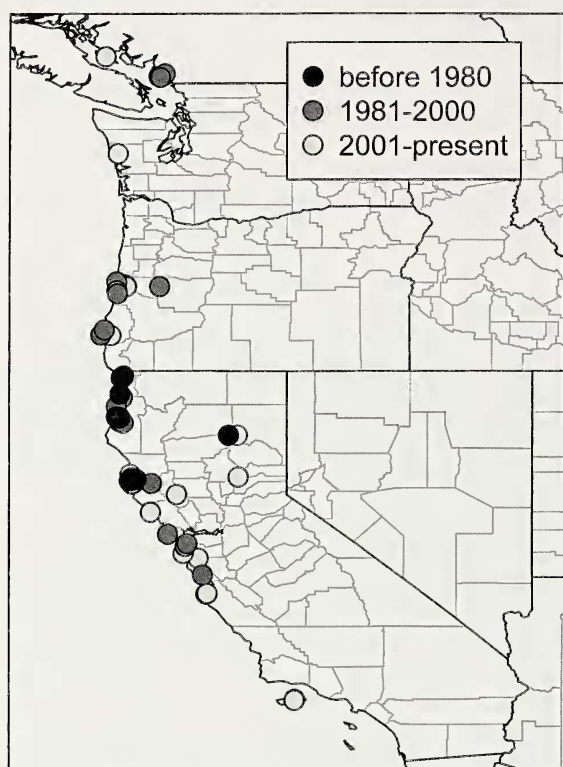


FIG. 1. Distribution of *Campylopus introflexus* in North America.

By the year 2000, *C. introflexus* had been documented along the coast from southern British Columbia to the Monterey Bay region, and in the last decade populations have been documented as far south as Santa Cruz Island and inland to Plumas National Forest. Throughout much of its distribution, and most notably in southern populations, *C. introflexus* is often associated with closed cone coniferous forests, especially Bishop Pine (*Pinus muricata* D. Don) forests (e.g., Christy Pines on Santa Cruz Island, Santa Barbara Co., CA; Del Monte Forest on the Monterey Peninsula, Monterey Co., CA; Salt Point State Park, Sonoma Co., CA; Pygmy forests of Mendocino Co., CA). Northern occurrences in Oregon and British Columbia are typically associated with nutrient poor sand dune soils, waterlogged soils of bogs and fens, or ruderal areas including roadsides, rooftops, and landscaped areas. The inland populations in Lassen Volcanic National Park are associated with hydrothermal areas (Showers 1978), while the other inland populations from Yuba Co. and Lake Co. are associated with highly disturbed areas (D. Toren, personal communication). Collections from disturbed environments constitute a large proportion of the records throughout the distribution, but several populations appear to be well established in otherwise undisturbed

vegetation. These include some of the populations in the pygmy forests around Fort Bragg and Mendocino, as well as the Santa Cruz Island population. Populations at the Del Monte Forest and Salt Point are mostly found in the immediate vicinity of hiking trails and unpaved roads. Clones can be robust, forming dense monospecific turfs to five centimeters thick or more and, in ideal conditions, several square meters or more in extent. Although no quantitative ecological data are available, these extensive patches appear to be outcompeting other bryophyte and lichen species.

Campylopus introflexus is reportedly dioicous (i.e., it has separate male and female gametophytes; Frahm 2007), however sporophytes have been observed in one of the northernmost populations at Burns Bog in southwestern British Columbia (Taylor 1997), from the southernmost population on Santa Cruz Island, and from the inland Boiling Springs Lake population. Given that the presence of sporophytes in a population implies colonization of at least two individuals (one male, one female), the presence of sporophytes throughout the distribution is noteworthy.

CONCLUSIONS

Campylopus introflexus has a well-documented history of invasion in Europe, and efforts there now focus on understanding the life history of the species and its impact on native ecosystems. In western North America much less is known due to the lack of adequate historical collections. With that important caveat, the existing collections are consistent with the expected pattern for a rapidly expanding distribution. While nothing is known about the potential of the species to impact the native flora in western North America, negative impacts in similar European ecosystems are well documented and should serve as a warning.

This study establishes baseline information on the currently known distribution and qualitative ecological preferences of the species. Future work should include efforts to increase awareness of botanists to introduced bryophytes, and implementation of quantitative ecological studies to better understand the ecosystem impacts and potential future distribution of *C. introflexus*. This is especially important in closed cone coniferous forests, and stabilized dune communities, both of which exist across relatively small areas and are rich in sensitive endemic vascular plants.

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APPENDIX 1

VOUCHER SPECIMENS, WITH LOCALITY, YEAR OF COLLECTION, AND HERBARIUM

CANADA. B.C.: Vancouver, 2010, *Joya* 609 (UBC); Texada Island, 2002, *Sadler s.n.* (UBC); Burns Bog, 1997, *Schofield* 107660 (DUKE, UBC); Burns Bog, 1997, *Schofield* 107661 (DUKE, UBC); Burns Bog, 1997, *Schofield* 107665 (UBC); Lulu Island, Richmond Nature Park, 2002, *Schofield* 120055 (DUKE, UBC); Lulu Island, W of Richmond Nature Park, 2006, *Schofield* 124572 (DUKE, UBC); Burns Bog, 1994, *Taylor s.n.* (UBC); Burns Bog, 1996, *Taylor* 96-2 (UBC); South Burnaby, near Byrne Rd, 1996, *Taylor* 96-9 (UBC); Lulu Island, W of Richmond Nature Park, 2002, *Taylor s.n.* (UBC).

USA. California. **Del Norte Co.:** Hwy 199 near Stoney Creek, 1971, *Chapman* 101 (UC); *Darlingtonia* bog 2 mi N of Gasquet, 1967, *Norris* 8167 (CAS); Gasquet, 1971, *Santana* 267 (UC). **Humboldt Co.:** Little River, near Airport, 1988, *Mishler* 3762 (Duke); Seashore 3 mi N of Manila, 1975, *Montalvo s.n.* (UC); Logging Rd S of Lumbar Hills, 1984, *Nelson* 7616 (UC); Humboldt State University Campus, 1979, *Norris* 53101 (UC); Bayside Golf Course, 1979, *Norris* 53102 (UC); Prairie Creek Redwoods State Park, 1980, *Norris* 56821 (UC); Greenwood Heights Rd ca 3.5 mi SE of Old Arcata Rd, 1981, *Norris* 58319 (UC); Freshwater Creek 2 mi SW of Kneeland, 1983, *Norris* 68275 (UC); Arcata City Forest 1 mi from Fickle Hill Rd, 1983, *Norris* 68751 (UC); Prairie Creek Redwoods State Park, 1984, *Norris* 71732 (UC); Hwy 101 Rest stop 5 mi N of Trinidad 1987, *Silver* 780 (UC); Sunny Brae, near Arcata, 1980, *Spjut* 6319 (UC). **Lake Co.:** Sulfur Bank Mine, near Clearlake, 2000, *Toren* 8027 (D. Toren, personal herbarium); Sulfur Bank Mine, near Clearlake, 2005, *Toren* 9383a (conf. B. Allen) (D. Toren, personal herbarium); Sulfur Bank Mine, near Clearlake, 2005, *Toren* 9383b (conf. B. Allen) (D. Toren, personal herbarium). **Marin Co.:** Limantour Beach, 1999, *O'Brien* 3353 (UC). **Mendocino Co.:** Pygmy Forest 1.2 mi E of Hwy 1 along Gibney Ln, 1998, *Becking*

98091118 (UC); Pygmy Forest 1.2 mi E of Hwy 1 along Gibney Ln, 1998, *Becking* 98091119 (UC); Logging Road 5 air miles E of Mendocino, 2007, *Carter* 2337 (UC); Pygmy forest east of Mendocino, 2007, *Carter* 2340 (UC); Mackerricher State Park 2007, *Carter* 2253 (UC); Pygmy forest near Airport SE of Mendocino 2007, *Carter* 2393 (UC); Pygmy Forest 2 mi from Hwy 101 along Rd 409, 1983, *Norris* 68762 (UC); Pygmy forest 1 mi E of Hwy 1 along Airport Rd, 1987, *Norris* 73153 (UC); Pygmy forest 6 mi E of Hwy 101 along Little Lake Rd, 1994, *Norris* 82496 (UC); Pygmy forest 6 mi. E of Hwy 101 along Little Lake Rd 1994, *Norris* 82502 (UC); Pygmy forest near Fort Bragg Airport, 2002, *Norris* 103725 (UC); Pygmy forest near Fort Bragg Airport, 2002, *Norris* 103731 (UC); Jackson State Forest, 3 mi E of Fort Bragg, 1971, *Selva* s.n. (UC); Pygmy forest near Albion, 2002, *Shevock* 21904 (CAS, UC); Pygmy forest near Albion, 2002, *Shevock* 21912 (CAS, UC); Pygmy forest at Sholar's Bog 2004, *Shevock* 24650 (CAS, UC); Fen area at Big River Laguna, 2004, *Shevock* 24676 (CAS, UC); Pygmy forest along Simpson Lane, 1976, *Showers* 3258 (UC); Mitchell Creek Rd 1 mi S of Simpson Lane, 1976, *Showers and Toren* s.n. (UC). **Monterey Co.:** Del Monte Forest, 2011, *Carter* 5942 (UC); Del Monte Forest, 2008, *Kellman and Lodder* 5921 (CAS); Pebble Beach, 2001, *Yadon* s.n. (UC). **Plumas Co.:** Lassen Volcanic National Park, Boiling Springs Lake, 2012, *Hutten* s.n. (M. Hutten, personal herbarium); Lassen Volcanic National Park, Terminal Geyser, 12 Oct 2012, *Hutten* s.n. (M. Hutten, personal herbarium); Boiling Springs

Lake, 1979, *Showers* 1909 (UC). **San Francisco Co.:** Mt. Davidson, 2000, *Toren* 7760 (CAS). **San Mateo Co.:** San Pedro Valley County Park, Montara Mt. Trail, 2009, *Shevock* 32699 (CAS). **Santa Barbara Co.:** Santa Cruz Island, *Christy* Pines, 2011, *Carter* 5330 (UC); Santa Cruz Island 1 mi W of Mt. Diablo, 2011, *Carter* 5954 (UC); Santa Cruz Island, Sierra Blanca Ridge, 2012, *Carter* 6686 (UC); Santa Cruz Island, Los Sauces Trail, 2002, *Robertson* 2154 (CAS). **Santa Clara Co.:** Geng Rd, Palo Alto, 2004, *Kellman* 3634 (CAS). **Sonoma Co.:** Salt Point State Park, 2012, *Carter* 6530 (UC). **Yuba Co.:** Along Oregon Hill Rd. near Greenville, 5 mi SE of Challenge, 2010, *Toren* 9735 (CAS).

USA. Oregon. **Coos Co.:** Muddy Lake, 8 km N of Langlois, 1981, *Christy* 3172 (DUKE, UBC). **Curry Co.:** Floras Lake State Park, 1981, *Christy* 3206 (DUKE, UBC); Floras Lake State Park, 1981, *Christy* 3207 (conf. Frahm) (UBC); 8 mi. north of Port Orford, 2006, *B. Shaw* 602 (DUKE); **Lane Co.:** Siuslaw NF, Oregon Dunes Recreation Area, 1993, *Christy* 8329 (UBC); Siuslaw NF, Oregon Dunes Recreation Area, 1993, *Christy* 8337 (UBC); Siuslaw NF, Sutton Recreation Area, 1999, *Christy* 9206 (UBC); Eugene, Lane Community College Campus, 1995, *Dorris* 1288 (UC); Florence, 2006, *B. Shaw* 593 (DUKE); Florence, 2006, *B. Shaw* 594 (DUKE); Florence, 2006, *B. Shaw* 595 (DUKE); Florence, 2006, *B. Shaw* 596 (DUKE).

USA. Washington. **Grays Harbor Co.:** Hwy 109 near Moclips, Township 21N, Range 11W, Section S29, 2001, *Hutten* 4952 (conf. Harpel 16 May 2002) (M. Hutten, personal herbarium).